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A REVISED DESCRIPTION OF THE SKULL OF
MOSCHORHINUS
(THERAPSIDA, THEROCEPHALIA)

By
J. F. DURAND

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A REVISED DESCRIPTION OF THE SKULL OF *MOSCHORHINUS* (THERAPSIDA, THEROCEPHALIA)

By

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(With 17 figures)

[Paper presented at the Palaeontological Society of southern Africa Symposium, Cape Town,
September 1986]

ABSTRACT

Certain aspects of the external morphology of the *Moschorhinus* skull have been misinterpreted or overlooked in previous studies. In this paper the external morphology of the posterior half of the *Moschorhinus* skull is discussed in detail. The bony elements forming the braincase and the morphology of the foramina, fossae and grooves visible on the exterior surface of the braincase are described, and their possible functions are discussed. Certain misconceptions concerning the morphology of the prootic, opisthotic, quadrate, pterygoid, squamosal and epipterygoid are corrected. In the light of these findings the taxonomic position of *Moschorhinus* relative to other therocephalians is discussed.

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INTRODUCTION

The interrelationships of the Therocephalia and their relationship with the Cynodontia are not adequately known. Certain authors, such as Broom (1938), Brink (1951), Hopson & Crompton (1969), and Kemp (1982), are of the opinion that the cynodonts had a therocephalian ancestor, whereas others such as Romer (1969) and Kermack & Kermack (1984) have argued that the cynodonts arose independently of the Therocephalia, from a more primitive ancestor. Most of the former authors accepted scaloposaur ancestry for the cynodonts, whereas Kemp (1972, 1982) argued that the cynodont ancestor was closely related to the whaitsiids.

To unravel therapsid phylogeny it is essential to know more about therocephalian morphology. The present study attempts to broaden our knowledge of

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Moschorhinus kitchingi, which is an interesting therocephalian with a mixture of primitive and advanced characteristics.

Moschorhinus seems to be more advanced than the pristerognathids and scaloposaurids, even though it has certain features in common with the gorgonopsians. *Moschorhinus* shares more characteristics with the whaitsiids than with any other therocephalian group. *Moschorhinus* is also more primitive than the whaitsiids but does not seem to be ancestral to them. The taxonomic position of *Moschorhinus* will be discussed in detail later.

The skull of *Moschorhinus* has been described by Broom (1920), Boonstra (1934), Brink (1959), and Mendrez (1974a). The elements forming the anterior half of the skull are well known from these descriptions. However, due to the poorly preserved braincase in most *Moschorhinus* specimens, or insufficient preparation thereof, certain misconceptions arose concerning the relations of the elements constituting the posterior half of the skull.

Two *Moschorhinus* skulls were selected for this study. Although these skulls are somewhat damaged and distorted, the posterior parts of the skulls are in such a condition that, with careful preparation it was possible to discover a wealth of information that adds to our knowledge of the *Moschorhinus* skull. In this paper the elements constituting the posterior half of the skull and the inter-relationships between these elements are described, and the possible courses of certain blood-vessels and nerves are discussed.

MATERIAL AND METHODS

Two previously undescribed specimens were selected for this study: *Moschorhinus kitchingi* (Broom) BP/1/2788 and BP/1/4636. BP/1/2788 was found by J. W. Kitching in Stoffelton, Afdeel Native Trust (now part of KwaZulu), near Bulwer, Natal, in the *Daptocephalus* zone (Kitching 1977) (*Dicynodon lacerticeps*-*Waitsia* Assemblage-zone—S.A.C.S. 1980). BP/1/4636 was found by J. W. Kitching on the farm Fairydale in the Bethulie district, Orange Free State in the *Lystrosaurus* zone (Kitching 1977) (*Lystrosaurus*-*Thrinaxodon* Assemblage-zone—S.A.C.S. 1980).

Moschorhinus kitchingi, BP/1/2788 (Figs 1–4)

Most of the matrix surrounding this skull had been removed with a hammer and chisel prior to this study. The matrix within the temporal cavities had not been removed. This distorted specimen is 21,5 cm long. The major parts of the skull roof and occiput are missing and the jugal and postorbital arches are damaged. Teeth are present in the damaged and distorted mandible. Aspects of this specimen's teeth and mandible were used in the reconstruction of the lateral view of the skull (Fig. 14).

Moschorhinus kitchingi, BP/1/4636 (Figs 5–11)

The whole skull was prepared for this study by means of an air-hammer and engraving tool. This distorted skull is 25 cm long. Parts of its jugal and post-

orbital arches are missing and the occiput is damaged. Although this skull is severely damaged, it yielded vital information. The descriptions and reconstruction of the posterior part of the skull and the dental formula are those of this specimen (Figs 12–17).

DESCRIPTION

The posterior half of the *Moschorhinus* skull consists of the following endochondral elements: the epipterygoid, prootic, opisthotic, quadrate, supraoccipital, exoccipital and basioccipital, and the following dermal elements: the squamosal, quadratojugal, jugal, interparietal, parietal, postorbital, tabular and pterygoid. The parasphenoid and basisphenoid are of endochondral and dermal origin.

The lateral wall of the braincase can be seen within the jugal arch (Fig. 16). The large parietal forms the sharp-crested roof of the braincase and the dorsal border of the temporal fossa. The posterior wall of the temporal fossa is largely formed by the squamosal. The medial wall of the temporal fossa is formed by the epipterygoid, the prootic, the ventrolateral part of the pterygoid, the lateral part of the opisthotic, and anterior parts of the supraoccipital and interparietal. Several features relating to blood-vessels and nerves can be seen within the temporal fossa.

The posterior surfaces of the parietal, interparietal and supraoccipital form the medial surface of the occiput, dorsal to the foramen magnum (Fig. 15). These elements are flanked by the tabulars, which cover part of the squamosal posteriorly. The lateral part of the occiput is formed by the posterior parts of the squamosal and the opisthotic. The foramen magnum is flanked by the exoccipitals. The ventromedial border of the occiput is marked by the basioccipital. Two of the most salient features of the occiput are the large post-temporal fenestra and the paroccipital fossa.

EPIPTERYGOID (Figs 12–14, 16)

In lateral view (Figs 14, 16), the flattened, blade-like epipterygoid can be seen. It contacts the parietal, supraoccipital and prootic dorsally and the pterygoid, prootic and squamosal ventrally. The upper part of the processus ascendens (dorsal lamina—Mendrez 1972, 1974a, 1974b) expands anteriorly to form an anterodorsal process and posteriorly to form a posterodorsal process. The basal part of the epipterygoid expands anteriorly to form an anteroventral process and posteriorly to form a posteroventral process (Mendrez 1972, 1974a, 1974b). A small posterior apophysis is present on the posterior edge of the processus ascendens, which probably made contact with the lateral part of the base of the anterodorsal process of the prootic (unfortunately damaged in all *Moschorhinus* specimens examined). The ventromedial part of the posterodorsal process of the epipterygoid contacts the anterolateral part of the anterodorsal process of the prootic just above the contact of the posterior apophysis with the prootic,



Fig. 1. *Moschorhinus kitchingi*. BP/1/2788. Dorsal view.



Fig. 2. *Moschorhinus kitchingi*. BP/1/2788. Ventral view.



Fig. 3. *Moschorhinus kitchingi*. BP/1/2788. Lateral view.



Fig. 4. *Moschorhinus kitchingi*. BP/1/2788. Oblique anterior view.

thus forming a circular foramen—the posterior foramen of the epipterygoid ('foramen veineux'—Mendrez 1974a) (see Fig. 16). There is a shallow funnel-like indentation surrounding the foramen on the lateral surface of the epipterygoid. A low ridge runs diagonally across the lateral surface of the epipterygoid from the tip of the posterodorsal process, passes anterior to the foramen, and terminates in the middle of the ventral part of the epipterygoid as a small tuberosity. This posterior foramen of the epipterygoid should not be confused with the dorsal venous foramen (see discussion). The dorsal border of the epipterygoid fits in snugly under the parietal. The central part of the dorsal border of the epipterygoid is overlapped laterally by the ventrolateral descending flange of the parietal. The tip of the posterodorsal process curves slightly downwards, away from the parietal, exposing the interparietal upon which the dorsal part of the posterodorsal process lies.

The anteroventral process of the epipterygoid is quite small in relation to the posteroventral process. It originates anteroventrally from the base of the processus ascendens. The anteroventral process terminates anteriorly to the dorsolateral ridge of the pterygoid and is in confluence with the posterior corner of this ridge. The term anteroventral process of the epipterygoid is preferred to the 'pterygoid process of the epipterygoid' (Crompton 1955) since the whole of the ventral border of the epipterygoid contacts the pterygoid. The foot of the epipterygoid covers the dorsal surface of the anterolateral third of the quadrate ramus of the pterygoid (see Figs 12, 16).

The posteroventral process of the epipterygoid originates at the base of the processus ascendens from where it flares out posterolaterally as an elongated, horizontal fan, overlying the middle third of the quadrate ramus of the pterygoid. These two processes are confluent laterally and posteriorly but not medially and anteriorly. The posteroventral process is slightly raised medially along its whole length, producing a medially facing groove that originates under the vertically inclined anterior part of the posteroventral process. The groove tapers off as it approaches the posterior border of the posteroventral process. The term posteroventral process of the epipterygoid is preferred to the 'quadrate process of the epipterygoid' (Crompton 1955), since it is doubtful whether the epipterygoid actually did contact the quadrate in *Moschorhinus*.

The posterior part of the posteroventral process of the epipterygoid is fan-shaped. The lateral half of the posterior border stretches across the dorsal surface of the quadrate ramus of the pterygoid. The posterior border contacts the anterior border of the anteroventral process of the squamosal medially, the contact being visible in dorsal and ventral views. This region of the epipterygoid forms part of the anterolateral corner of the pterygo-paroccipital foramen (see Figs 12, 13, 16).

In lateral view (Fig. 16), the ventral suture of the epipterygoid runs in the middle of the lateral side of the structure formed with the quadrate ramus of the pterygoid. The suture dips anteriorly and then curves upwards delimiting the border of the anteroventral process. Posteriorly the suture runs diagonally



Fig. 5. *Moschorhinus kitchingi*. BP/1/4636. Dorsal view.



Fig. 6. *Moschorhinus kitchingi*. BP/1/4636. Ventral view.

upwards in a straight line delimiting the ventral border of the posteroventral process laterally on the dorsal side of the quadrate ramus of the pterygoid.

The processus ascendens of the epipterygoid juts upwards and slightly inwards. The middle part of the processus ascendens is relatively constricted in comparison with the dorsal and ventral parts, giving the epipterygoid an hour-glass shape in lateral view. The ventral part of the epipterygoid is directed outwards posteriorly and inwards anteriorly. This closely reflects the orientation of the quadrate ramus of the pterygoid, whereas the dorsal part of the epipterygoid is more parasagittally inclined.

A very distinct and large cavum epiptericum is present, bordered medially by the anteroventral process of the prootic and laterally by the epipterygoid. Certain nerves and veins traverse the cavum epiptericum (see discussion).



Fig. 7. *Moschorhinus kitchingi*. BP/1/4636. Left lateral view.



Fig. 8. *Moschorhinus kitchingi*. BP/1/4636. Right lateral view.



Fig. 9. *Moschorhinus kitchingi*. BP/1/4636. Occipital view.

PROOTIC (Figs 12–17)

The prootic and opisthotic are two separate elements. The sutures dividing these bones will be discussed later.

The prootic is a complex bone with five major processes. The terminology used by Mendrez (1972) to describe these processes will be followed here. The prootic meets the basisphenoid ventrally, the squamosal and opisthotic posterolaterally, the epipterygoid anterolaterally, and the supraoccipital dorsally.

In lateral view (Fig. 16), two distinct ridges can be seen running diagonally across the prootic, more or less parallel to each other. The ridge running from the central process to the anterodorsal process is here called the central ridge of the prootic (the 'delicate rising crest' of Mendrez 1972: 205). The ridge running from the lip of the fenestra ovalis to the anteroventral process of the prootic, is here called the ventral ridge of the prootic (the 'sharp crest'—Mendrez 1972: 203; the 'strong crest'—Mendrez 1972: 205; 1974b: 76).

In lateral view it can be seen that the prootic has two distinct anterior processes directed diagonally anterodorsally, viz: the anterodorsal process above and anteroventral process below. These two processes are separated by the incisura prootica. Olson (1944), Crompton (1955), Mendrez (1972) and others used these terms to describe the anterior part of the prootic.

The anterior part of the anterodorsal process makes contact with the medial surface of the epipterygoid, whereas the anteroventral process passes medially to the epipterygoid, forming a large vacuity between it and the epipterygoid—



Fig. 10. *Moschorhinus kitchingi*. BP/1/4636. Detail of left temporal region.



Fig. 11. *Moschorhinus kitchingi*. BP/1/4636. Dorsolateral view of left temporal region.

the cavum epiptericum, which will be discussed later. The anterodorsal process runs more or less parallel to the sagittal plane, whereas the anteroventral process points inwards.

The anterodorsal process of the prootic (processus anterior superior—Siebenrock 1893; posterior prootic process—Boonstra 1934) is a flattened, broad, projection that originates more or less in the middle of the prootic. Its dorsal border is continuous with the dorsal border of the rest of the prootic, and its ventral border is a continuation of the central ridge of the prootic. The anterodorsal process is rather broad posteriorly but tapers anteriorly, the thinnest part being its anterior edge, which contacts the posteromedial edge of the epipterygoid laterally. This region is damaged in the specimen described by Mendrez (1974a). The anteroventral edge of the anterodorsal process forms the posterior border of the posterior foramen of the epipterygoid. There is a slight lateral protrusion on the posterior part of the ventral border of the anterodorsal process, causing a ventrolaterally directed protuberance in the central ridge of the prootic. This is probably where the prootic made contact with the posterior apophysis of the epipterygoid, because of its inclination towards, and proximity to, the apophysis.

Bordering the anterodorsal process of the prootic dorsally and meeting the anterodorsal process of the epipterygoid is the flat, finger-like anterolateral process of the supraoccipital. The suture between the supraoccipital and prootic is not continuous. Posterior to the ventral edge of the posterodorsal process of the epipterygoid, a small triangular gap is formed between the supraoccipital and prootic. This is the dorsal venous foramen commonly found in many therapsids (see discussion).

The plane of the anterodorsal process is diagonally inclined in cross-section. The ventral border flares out laterally, whereas the dorsal border is medially inclined, reflecting the orientation of the epipterygoid.

The anteroventral process of the prootic (processus anterior inferior—Siebenrock 1893; anterior prootic process—Boonstra 1934) originates below the contact between the posterior apophysis of the epipterygoid and the anterodorsal process. This process is the ossified pila antotica (pleurosphenoid) (De Beer 1937; Olson 1944; Säve-Söderbergh 1947; Crompton 1955). The dorsal border of the anteroventral process curves upwards in a crescent shape. The anteroventral process is vertically inclined in cross-section and curves inwards anteriorly. The anteroventral process is traversed anteriorly by a horizontal groove. Above this shallow indentation, a low ridge runs from the posterior border of the incisura prootica anteriorly. This low ridge flares out anteriorly, forming two small, anteriorly jutting projections.

The incisura prootica is wide and deep. It is bordered ventrally by the concave dorsal border of the anteroventral process and dorsally by the straight ventral border of the anterodorsal process.

The foramen for the facial nerve (VII) is situated between the central and ventral ridges of the prootic. This foramen is nearer the former ridge and on the

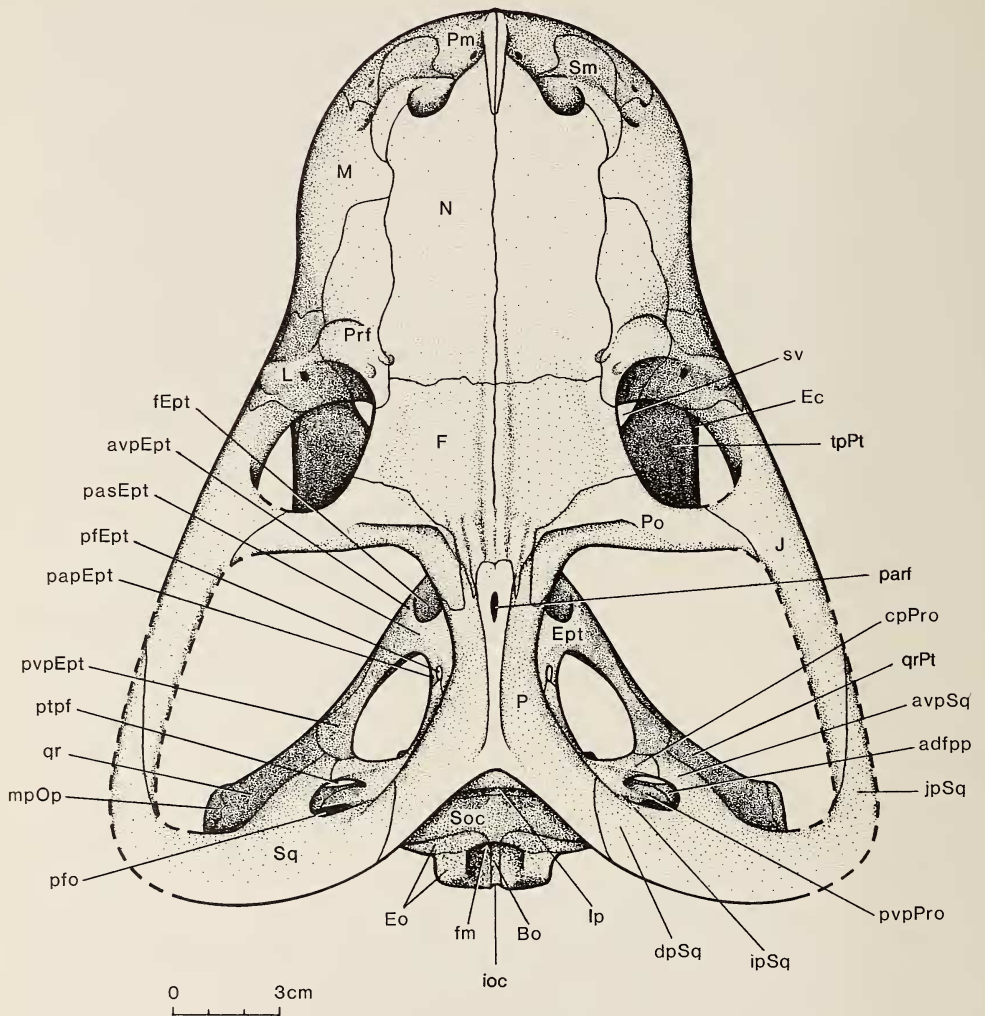


Fig. 12. *Moschorhinus kitchingi*. Dorsal view.

same level as the ventral border of the anteroventral process of the prootic anterior to it, and the central process of the prootic posterior to it.

There is a small ventral notch between the ventral border of the anteroventral process and the braincase floor. Its posterior border is formed by the anterior border of the basal region of the prootic. The ventral border is formed by the basisphenoid. This is the same as the notch described by Crompton (1955) for the Scaloposauridae, though here it is more open anteriorly.

The prootic has three prominent lateral processes of approximately the same length. The central process of the prootic (lateral process of the prootic—

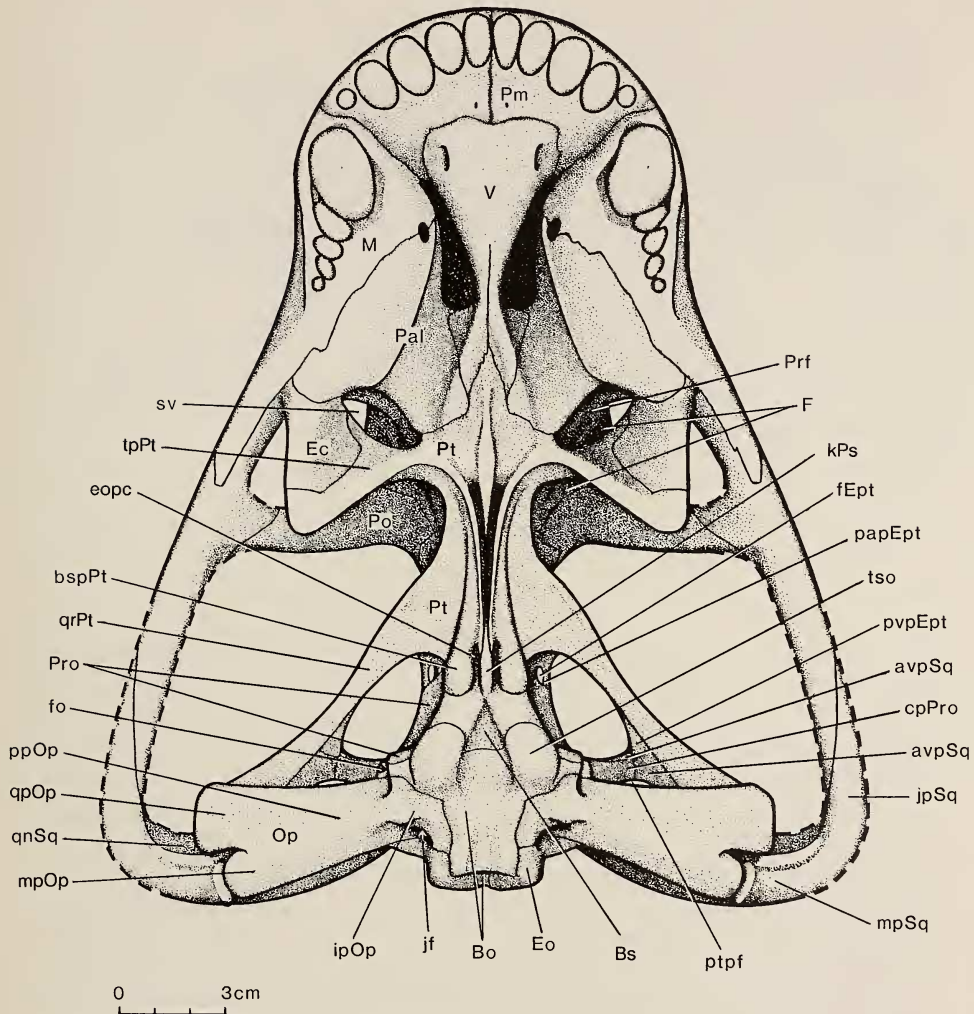


Fig. 13. *Moschorhinus kitchingi*. Ventral view.

Kemp 1972) can be seen in lateral (Fig. 16), dorsal, ventral and occipital views. It juts out laterally and slightly posteroventrally towards the squamosal. Its anterolateral corner contacts the posteromedial corner of the posteroventral process of the epipterygoid. The medial part of the anteroventral process of the squamosal (prootic process of the squamosal—Mendrez 1974b) contacts this central process in a complex manner: the distal part of the central process forms two flanges, one anterodorsally, the other posteroventrally, between which the thin medial blade of the anteroventral process of the squamosal is wedged.

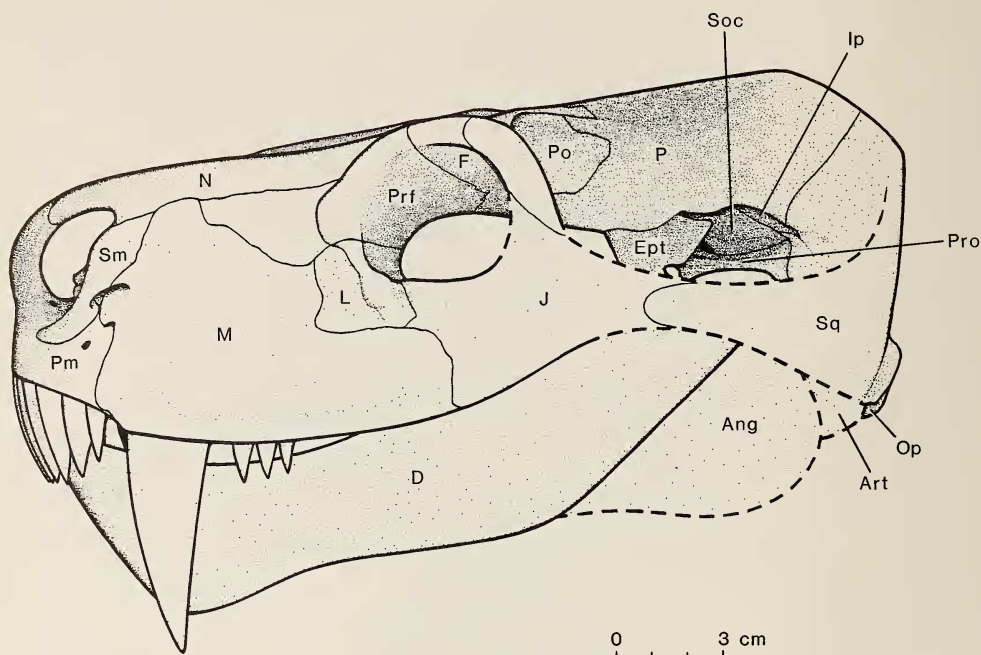


Fig. 14. *Moschorhinus kitchingi*. Lateral view.

These two elements form an anterodorsally curving bar that forms the anterior border of the pterygo-paroccipital foramen. The dorsal crest-like border of this bar is a continuation of the central ridge of the prootic. The anteroventral border of this bar forms a sharp concave crest running from the dorsal lip of the fenestra ovalis medially to the posteromedial corner of the posteroventral process of the epipterygoid laterally. The distal part of the central process is spindle-shaped in cross-section. The base of the central process, however, is triangular in cross-section, because of a short, sharp crest that forms the posteromedial corner of the process. This crest originates on the posteromedial part of the central process, curves posteromedially and terminates on the anterior surface of the posteroventral process of the prootic.

Behind the central process of the prootic, a more posteriorly inclined, flattened process, the posteroventral process of the prootic, originates. This process can be seen in occipital view. It contacts the opisthotic ventrolaterally. This unified structure forms the posterior wall of the pterygo-paroccipital foramen, the ventral border of the post-temporal fenestra and the anterior wall of the paroccipital fossa. The posteroventral process forms only the dorsomedial quarter of the posterior wall of the pterygo-paroccipital foramen and the medial half of the ventral border of the post-temporal fenestra.

A third process, the posterodorsal process of the prootic, contacts the intermediate process of the squamosal dorsally. It can be seen in lateral view

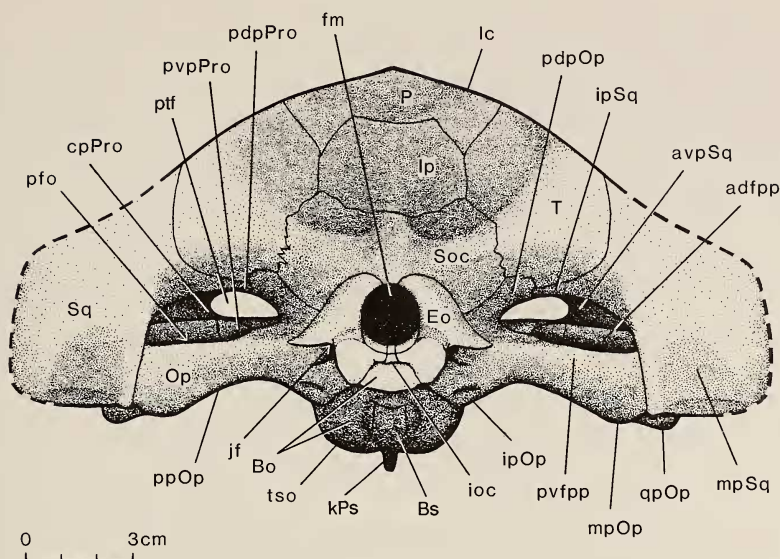


Fig. 15. *Moschorhinus kitchingi*. Occipital view.

(Fig. 16). The posterodorsal process forms most of the anterodorsal rim of the post-temporal fenestra. This process tapers off from a relatively broad base medially to a point jutting laterally, terminating in the lateral part of the roof of the post-temporal fenestra. This process protrudes from under the intermediate process of the squamosal anteromedially but, as it progresses laterally, it is gradually covered by the intermediate process of the squamosal anteriorly. Its posteromedial half is covered by the posterodorsal process of the opisthotic.

In lateral (Figs 16, 17) and ventral (Fig. 13) views, it can be seen that the basal region of the prootic is in sutural contact with the basisphenoid. The lateral suture runs diagonally from the floor of the braincase anterodorsally to the fenestra ovalis posteroventrally. The anterodorsal part of the lip surrounding the fenestra ovalis is formed by the basal region of the prootic (see Fig. 17).

As Mendrez (1972, 1974a) has remarked, the opisthotic and prootic are two quite separate bones. A clearly distinguishable suture divides them. The posterodorsal process of the opisthotic does not make contact with the lateral border of the posterodorsal process of the prootic, nor is it visible in anterior view as Mendrez (1974a) stated to be the case. The posterodorsal process of the opisthotic covers the posteromedial half of the posterodorsal process of the prootic posteriorly. In occipital view, one can observe within the post-temporal fenestra a part of the suture dividing the posterodorsal processes of the prootic and the opisthotic. This suture runs vertically for a short distance, skirting the lateral border of the posterodorsal process of the opisthotic, and then curves medially along its ventral border to where the posteromedial borders of the posteroventral and posterodorsal processes of the prootic originate. Laterally to

this, the suture divides the medial lip formed by the posteroventral process of the prootic and the posteroventral flange of the paroccipital process of the opisthotic. Ventrally to this medial lip, the suture that divides the posteroventral process of the prootic from the anterodorsal flange of the opisthotic, runs laterally. It can be traced posteriorly in the paroccipital fossa (Mendrez 1972: 203) and anteriorly between the anterodorsal flange of the paroccipital process of the opisthotic and the posteroventral process of the prootic. The suture curves first ventrally then medially along the border of the posteroventral process of the prootic. The suture then skirts the base of the central process of the prootic anteroventrally and the posterior corner of the dorsal lip of the fenestra ovalis, before it enters the roof of the fenestra ovalis medially (see Fig. 17).

The concave, dorsal border of the prootic can be seen in lateral view, curving posterodorsally to meet the medial border of the intermediate process of the squamosal. The central part of the dorsal border of the prootic (dorsal limit of the 'lame dorsale' of the prootic—Mendrez 1974a) contacts the supraoccipital. The largest part of the ventral border of the lateral supraoccipital fossa is formed by the dorsal border of the prootic. (This fossa is discussed below.)

OPISTHOTIC (Figs 12–17)

The opisthotic contacts the exoccipital and basioccipital posteromedially, the prootic anteromedially, the tabular, supraoccipital and squamosal dorsally, the squamosal, pterygoid and quadrate laterally, and the stapes ventrally.

The opisthotic consists of a robust transverse bar—the paroccipital process, a T-shaped ventromedial tuberosity—the internal process, and a small, flattened dorsomedial projection—the posterodorsal process. This is the terminology Mendrez (1972, 1974a, 1974b) used to describe the opisthotic.

The paroccipital process of the opisthotic is V-shaped in parasagittal section. This V-shaped process is formed by two flanges joined anteroventrally. The posteroventral flange is more massive than the anterodorsal flange. The V-shaped cavity formed by these two flanges is the paroccipital fossa of the opisthotic. This fossa can be seen in dorsal and occipital views (Mendrez 1972, 1974a, 1974b).

The paroccipital process is laterally subdivided into two processes that can be distinguished in ventral view, viz: the mastoid process of the opisthotic posteriorly, and the quadrate process of the opisthotic anteriorly (see Fig. 13).

The mastoid process is marked by a ventral ridge originating approximately in the middle of the paroccipital process and terminating near the bulbous lateral end of the mastoid process. This ventrolaterally curving ventral ridge adds to the robustness of the mastoid process. The mastoid process is thickest near its distal end where the ventral ridge terminates. The posterior margin of the mastoid process marks the posteroventral border of the rim of the paroccipital fossa. The posterolateral part of the mastoid process contacts the squamosal laterally, whereas its anterolateral part is free. A shallow indentation

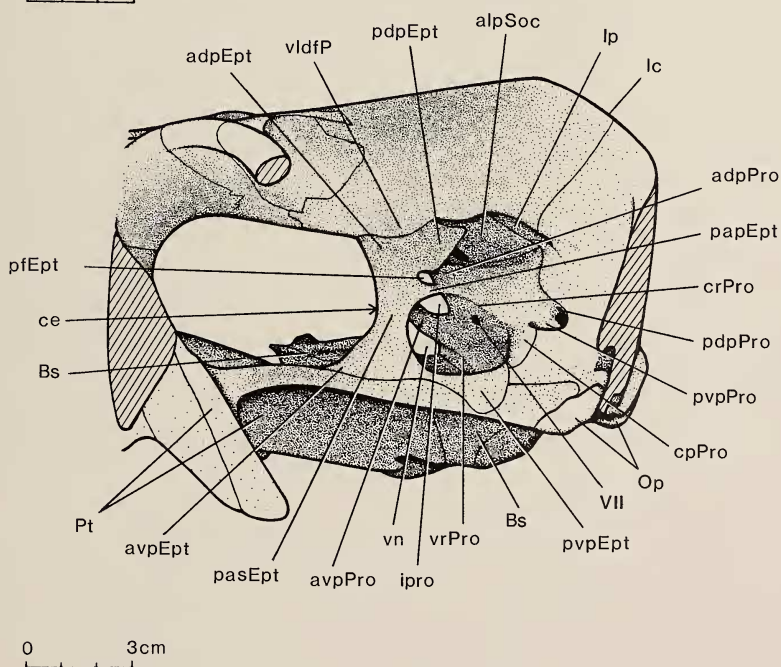
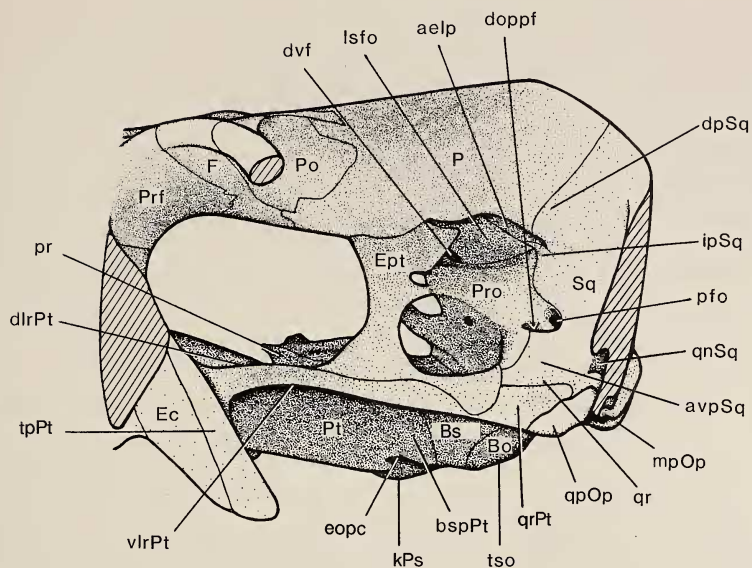


Fig. 16. *Moschorhinus kitchingi*. A. Detail of left temporal region. B. Detail of left temporal region.

separates the mastoid and quadrate processes of the opisthotic and forms the so-called roof of the middle ear ('*toit de l'oreille moyenne*'—Mendrez 1974a). The quadrate process of the opisthotic, which juts outwards anterolaterally, is thinner, broader and longer than the mastoid process. It becomes broader laterally, similarly to the mastoid process, to form a bulbous lateral end. The quadrate process projects further laterally than the mastoid process. The posterior third of the dorsolateral surface of the quadrate process of the opisthotic contacts the quadrate process of the squamosal and the anterior two-thirds contact the posterior part of the quadrate ramus of the pterygoid. This can be seen in lateral (Fig. 16) and dorsal (Fig. 12) views. The lateral surface of the quadrate process of the opisthotic loosely articulates with the quadrate and its anteroventral surface loosely contacts the stapes.

The anterodorsal flange of the paroccipital process (anterior wall of the paroccipital process—Mendrez 1972) contacts the posteroventral process of the prootic medially. This combined structure forms the posterior wall of the pterygo-paroccipital foramen (seen in dorsal view), the ventral border of the post-temporal fenestra and the anterodorsal border of the paroccipital fossa (both seen in occipital view). The anterior ridge of the paroccipital process, marking the anterior border of the opisthotic, originates at the anterolateral edge of the quadrate process of the opisthotic and terminates near the dorsal lip of the fenestra ovalis. The base of the central process of the prootic and the dorsal lip of the fenestra ovalis (also formed by the prootic) contact the anteromedial part of the opisthotic (see Fig. 17). The suture dividing the prootic and opisthotic has already been described.

The opisthotic forms the posterior third of the fenestra ovalis. The suture dividing the opisthotic and the basioccipital can be seen in ventral and occipital view. It emerges from the posteroventral corner of the fenestra ovalis and then turns medially across the ventral surface of the lip of the fenestra ovalis (Fig. 17). The suture then curves posteromedially behind the tuberculum spheeno-occipitale, runs around the internal process of the opisthotic and then curves laterally after passing medially to the jugular foramen. On reaching the posteroventral lip of the jugular foramen, the suture extends into the jugular foramen in an anterodorsal direction.

The internal process of the opisthotic can be seen in ventral and occipital views. It is formed by a ridge originating on the ventromedial part of the paroccipital process, curving and expanding ventromedially and terminating as a ventromedial tuberosity between the jugular foramen and fenestra ovalis. From this tuberosity a thin anterolateral and thicker, blunter posteromedial extension project. The posterior extension forms the ventral lip of the jugular foramen and the anterior extension forms the posteroventral corner of the lip of the fenestra ovalis (Fig. 17). There is a small groove dividing the anterior extension from the medial part of the opisthotic that forms the posterior border of the fenestra ovalis. Similarly the posterior extension is separated ventrally from the part of the opisthotic that forms the anterior part of the roof of the jugular foramen by

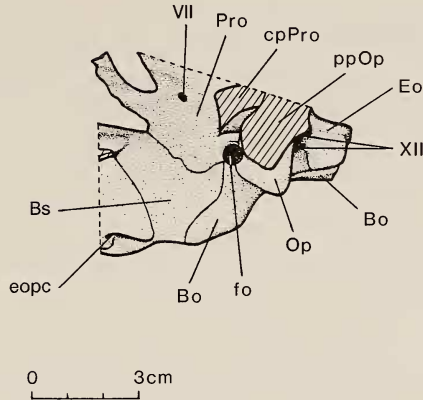


Fig. 17. *Moschorhinus kitchingi*. Detail of left fenestra ovalis.

a shallow groove (see Fig. 17). This groove runs from inside the jugular foramen anteromedially, more or less parallel to the ventrolateral suture of the exoccipital, and terminates on the posteromedial surface of the paroccipital process. The part of the opisthotic that is overlain by the posterior extension of the internal process projects into the jugular foramen and, with the exoccipital posteriorly, forms the roof of the jugular foramen. A short groove is present on the posterior face of the ridge and tuberosity, ventral to the groove at the jugular foramen (see Figs 13, 15).

In occipital view, the suture between the anterolateral part of the exoccipital and the posteromedial surface of the opisthotic can be seen. This suture runs from inside the jugular foramen, around the exoccipital ventrolaterally, and then dorsomedially. Also visible in occipital view is the suture dividing the medial corner of the posterodorsal process of the opisthotic and the ventrolateral corner of the supraoccipital. It originates half-way along the dorsal border of the exoccipital.

The posterodorsal process of the opisthotic (visible in occipital view) originates medially to the paroccipital fossa and the lip (formed by the posteroventral process of the prootic and the posteroventral flange of the paroccipital process) covering the dorsomedial part of the paroccipital fossa. The posterodorsal process of the opisthotic is a flat projection that curves dorso-laterally. It forms the posteromedial surface of the post-temporal fenestra. Its lateral border stretches as far medially as the lip covering the dorsomedial part of the paroccipital fossa (a medial indentation separates these two structures). The posterodorsal process of the opisthotic makes sutural contact along its dorsomedial border with the supraoccipital. This suture continues in a dorso-lateral direction as it follows the dorsal border of the posterodorsal process. The suture dividing the supraoccipital and tabular originates half-way along this border. Part of the dorsal border of the posterodorsal process contacts the

ventral border of the tabular. The lateral border of the posterodorsal process contacts the posteroventral part of the intermediate process of the squamosal. The short ventral border of the posterodorsal process of the opisthotic contacts the posterior part of the posterodorsal process of the prootic. The posterodorsal process of the opisthotic is not visible in anterior view as Mendrez (1974a) has observed in *Moschorhinus kitchingi*, SAM-K118. It rather resembles the condition found by Mendrez (1974b) in *Promoschorhynchus platyrhinus*, RC 116, where the posterodorsal process is completely covered anteriorly by the intermediate process of the squamosal and the anterodorsal process of the prootic.

SQUAMOSAL (Figs 12–16)

The squamosal is a large, complex bone with several processes; the terminology used by Mendrez (1972) will be used to describe these processes. The squamosal makes contact with the parietal, interparietal, supraoccipital, prootic, opisthotic and tabular medially, the pterygoid and epipterygoid anteriorly, and with the jugal and quadrate laterally.

The major part of the posterior wall of the temporal fossa is formed by the three large medial processes of the squamosal. The laterally sloping dorsal border of the squamosal forms the posterodorsal border of the temporal fossa and anterior part of the lambdoid crest. The three medial processes occur one above the other (see Fig. 16). The anteroventral process (third squamosal process—Crompton 1955) is separated from the intermediate process (second squamosal process of Crompton) by the post-temporal fenestra. The intermediate and dorsal processes (first squamosal process of Crompton) are separated by the posterior fold forming part of the lateral supraoccipital fossa.

The medial part of the broad dorsal process of the squamosal covers the posterolateral part of the parietal (see Fig. 12). The lateral surface of the dorsal process is confluent with that of the parietal, as are their dorsal and ventral borders. The dorsal process of the squamosal is fused to the tabular along most of its posterior surface. Its ventral border is marked by the fold forming the posterior part of the lateral supraoccipital fossa (see Fig. 16). Part of this fold is occupied by the anterior extension of the interparietal, which contacts the ventral border of the dorsal process posterodorsally.

In lateral view it can be seen that the dorsal border of the intermediate process of the squamosal forms the ventral border of the above-mentioned fold and contacts the posteroventral area of the part of the interparietal that is laterally exposed. The anterior part of the intermediate process makes sutural contact with the anterolateral process of the supraoccipital dorsally and with the prootic ventrally. The medial part of the ventral border of the intermediate process of the squamosal forms a V-shaped notch in which the posterodorsal process of the prootic is wedged. This fused structure forms the dorsomedial part of the roof of the post-temporal fenestra, whereas the dorsolateral part of the roof is formed by the lateral part of the ventral border of the intermediate process.

In occipital view it can be seen that the medial part of the intermediate process contacts the ventrolateral part of the tabular, and the dorsolateral part of the posterodorsal process of the opisthotic ventromedially.

In lateral view the ventral border of the intermediate process can be seen. It curves ventrolaterally in a crescent-shape, delimiting the dorsolateral rim of the post-temporal fenestra, until it becomes the dorsal border of the anteroventral process of the squamosal. The dorsal border of the anteroventral process forms the lateral part of the pterygo-paroccipital foramen. The medial blade of the anteroventral process of the squamosal (the prootic process of the squamosal—Mendrez 1974*b*) is wedged into a V-shaped notch formed by the lateral part of the central process of the prootic. The posteromedial border of the posteroventral process of the epipterygoid contacts the anteroventral process of the squamosal anteromedially. The whole anterolateral border of the anteroventral process of the squamosal, except for its distal end, contacts the posteromedial edge of the quadrate ramus of the pterygoid. This suture runs posterolaterally from the contact between the posterior part of the posteroventral process of the epipterygoid and the squamosal, to the suture connecting the squamosal and opisthotic.

The laterally directed flange of the squamosal overlies most of the opisthotic, the only contact formed being where their distal borders meet (see Fig. 15). The ventrolateral part of the anteroventral process of the squamosal (the quadrate process of the squamosal—Mendrez 1974*b*) contacts the dorsal part of the posterolateral tip of the quadrate process of the opisthotic posterior to the squamosal-ptyerygoid contact (see Fig. 16). This suture is visible anteriorly to the quadrate notch in the squamosal. (This notch is described below.) The ventrolateral part of the squamosal seen in occipital view is the mastoid process of the squamosal. The suture connecting the dorsolateral border of the mastoid process of the opisthotic to the ventromedial border of the mastoid process of the squamosal is visible in occipital and ventral views. Except for these two above-mentioned distal sutures and the suture with the posterodorsal process of the opisthotic, the rest of the squamosal overlies, but does not contact, the opisthotic. It thus forms the lateral parts of the roof of the pterygo-paroccipital foramen and the roof of the paroccipital fossa.

A deep, dorsally directed quadrate notch of the squamosal is present anteriorly, in the distal part of the squamosal; it houses the dorsal part of the quadrate (see Fig. 16). This notch is surrounded by the jugal laterally, the posterolateral part of the anteroventral process of the squamosal (which covers the quadrate process of the opisthotic) anteroventrally and the thick lip formed by the jugal process of the squamosal dorsally. A shallow indentation is present anteroventrally to this notch in the bones covering the quadrate process of the opisthotic, namely, the quadrate process of the squamosal and the posterior end of the quadrate ramus of the pterygoid. This indentation, the quadrate recess of the squamosal, is probably synonymous with that described by Kemp (1969) and with the squamosal recess ('recessus squamosal') of Mendrez (1974*a*). The

posterior part of the quadrate fits into this recess. The quadrates are lost in most of the *Moschorhinus* specimens, because they were loosely articulating bones with no sutural connections.

In occipital view the following features can also be seen: the posteroventral border of the intermediate process of the squamosal curves ventrolaterally, forming the posterolateral border of the post-temporal fenestra and part of the posterolateral border of the paroccipital fossa. A ridge runs in a dorso-ventral plane on the mastoid process of the squamosal laterally to its contact with the opisthotic. A posteroventral facing indentation on the mastoid process of the squamosal borders this ridge laterally. Ventrally to this indentation and ridge, and medially to the posterior part of the quadrate, a notch is situated posteriorly between the two lateral processes of the opisthotic.

The dorsolateral part of the squamosal (the jugal process) curves anteriorly to join the posterior end of the jugal. Unfortunately, in those specimens studied, the jugal arch is either lost or damaged to such a degree that a detailed description is impossible.

SUPRAOCCIPITAL AND INTERPARIETAL (Figs 14, 15)

Both the supraoccipital and the interparietal are visible in occipital and lateral view. In occipital view, the broad supraoccipital contacts the interparietal dorsally, the tabulars dorsolaterally, the posterodorsal processes of the opisthotics ventrolaterally and the exoccipitals ventrally. The exoccipitals cover the ventromedial part of the supraoccipital, except for a narrow gap between the exoccipitals where the supraoccipital forms the dorsomedial part of the roof of the foramen magnum. The suture between the tabular and supraoccipital runs diagonally in a dorsomedial direction from its origin at the junction of the ventral borders of the tabular and supraoccipital, to the dorsal border of the supraoccipital. The suture between the ventral border of the interparietal and the dorsal border of the supraoccipital is horizontal and short. A large, deep occipital indentation is present in the region of the interparietal. Two smaller, ventral indentations, forming part of the larger indentation, are present on the dorsal part of the supraoccipital. These flank a short ridge originating in the middle of the dorsal part of the supraoccipital and continuing dorsally on the interparietal.

In occipital view, the interparietal is a small, laterally ovate bone bordered ventrally by the supraoccipital, laterally by the tabulars and dorsally by the parietal.

The aforementioned occipital indentation causes the interparietal, parietal, medial part of the tabular, and the dorsal part of the supraoccipital to be set deeper than the rest of the surrounding elements. This indentation was for the attachment of certain neck muscles.

In lateral view, ventral to the posteromedial angle of the temporal foramen (Mendrez 1974a: 80), is the lateral supraoccipital fossa, a large oval indentation bordered dorsally by the parietal, whose ventral border forms a concave over-

hang. The ventral border of this fossa is formed by the concave dorsal edge of the anterodorsal process of the prootic, and the anterior border by the anteroventrally curving posterior edge of the posterodorsal process of the epipterygoid. The fossa tapers off posteriorly into a short, horizontal fold. The anteromedial part of the intermediate process of the squamosal forms the posterior border of the fossa and the ventral part of its posterior fold. The dorsal border of this fold is formed by the ventral border of the parietal and the dorsal process of the squamosal. The dorsal venous foramen is situated in the anterior region of this fossa.

The anterior extensions of the supraoccipital and interparietal are visible within the lateral supraoccipital fossa. The anterolateral process of the supraoccipital lies at a more medial level than any of the surrounding elements, forming the medial wall of the lateral supraoccipital fossa. The anterolateral process of the supraoccipital contacts the parietal dorsally, the posterodorsal process of the epipterygoid anteriorly, the anterodorsal process of the prootic ventrally, the intermediate process of the squamosal posteroventrally, and the anterior extension of the interparietal posterodorsally. The dorsal venous foramen is visible ventral to the epipterygoid-supraoccipital contact and anterior to the prootic-supraoccipital contact.

The anterior extension of the interparietal fills the posterodorsal corner of the lateral supraoccipital fossa. The interparietal is triangularly shaped and contacts the anterolateral process of the supraoccipital anteroventrally, the dorsal border of the intermediate process of the squamosal posteroventrally, the ventral border of the parietal anterodorsally, and the ventral border of the dorsal process of the squamosal posterodorsally.

PARIETAL (Figs 12, 14–16)

The parietal forms the posterodorsal part of the skull. It contacts the squamosal and tabular posteroventrally, the prootic and epipterygoid ventrolaterally, the postorbital anterolaterally, and the frontal anteriorly.

In occipital view the parietal is situated between the dorsomedial borders of the tabulars and the dorsal border of the interparietal. Its dorsal border is in confluence with those of the tabular and squamosal. These borders form the ventrolaterally curving, dorsal border of the occiput.

The parietal has a pronounced sagittal crest. The anterodorsal rim of the temporal fossa is formed by an acute curving ridge on the posterodorsal and dorsolateral surfaces of the postorbital (see Fig. 12). These postorbital ridges bow posteriorly and are continued on the dorsomedial surface to produce the sagittal crest. The sagittal crest is widest at its origin, anterior to the parietal foramen. Posteriorly it becomes narrower and splits into two posterolaterally flaring lambdoid crests, which form the dorsomedial border of the occiput posteriorly and part of the posterodorsal rim of the temporal fossa laterally.

The parietal, in dorsal view, has an hour-glass shape. It is broad and robust anteriorly, constricted in the middle above the epipterygoid, and forms two

posterolaterally flaring flanges that form the anterior parts of the lambdoid crests.

The broad anterior part of the parietal contacts the frontal and postorbitals (see Figs 12, 14, 16). In dorsal view, it can be seen that the suture between the posterodorsal border of the frontal and the anterodorsal border of the parietal has a zig-zag arrangement. The anteroventrally sloping area between the anterior border of the parietal and the parietal foramen, i.e. the broad origin of the sagittal crest, is corrugated. In BP/1/4636, four small but distinct parasagittal ridges are present in this region. The two medial ridges join up with the sagittal ridge of the frontal anterior to them. This sagittal ridge runs on the dorsal surface of the skull, from the middle of the nasals, over the frontals, and joins the medial ridges of the parietal, which terminate on the slope anterior to the parietal foramen.

The posteromedial flange of the postorbital and the anterolateral part of the parietal are separated by a suture that can be seen in dorsal and lateral view.

The parietal foramen for the pineal organ is situated in the anterior part of the sagittal crest, on the same level as the posterior border of the posteromedial flange of the postorbital (see Fig. 12). The external opening of the parietal foramen is a narrow spindle-shaped slit, similar to the condition in the *Moschorhinus* specimens described by Brink (1959) and Mendrez (1974a).

In lateral view, the vertically curving suture between the dorsal process of the squamosal and the posterior flange of the parietal can be seen. This suture closely reflects the occipital suture between the parietal and interparietal and the tabular. The ventral border of the parietal forms the roof of the braincase. The anterior third of the ventral border of the parietal does not make sutural contact with any bony elements, since this part of the braincase was unossified. The middle part of the parietal is triangular in cross-section. The lateral edges of the ventral border of this triangle contact the dorsal border of the epipterygoid and the dorsal part of the anterolateral process of the supraoccipital on each side. The short ventrolateral descending flange of the parietal overlaps the anterior two-thirds of the dorsal border of the epipterygoid. The posterior part of the ventral area of the parietal contacts the dorsal border of the interparietal. The ventrolateral edge of the parietal, posterior to its suture with the epipterygoid, forms the dorsal border of the lateral supraoccipital fossa.

EXOCCIPITAL (Figs 12, 13, 15, 17)

In occipital view, it can be seen that the exoccipital contacts the posteroventral part of the supraoccipital dorsally, the posteromedial part of the opisthotic laterally, and the posterior part of the basioccipital ventromedially. The concave medial side of the exoccipital forms the lateral wall of the foramen magnum.

The exoccipital is divided externally into a flat anterodorsal part and a posteroventral boss. The ventrolateral half of the anterodorsal part overlaps the posteromedial part of the opisthotic and the dorsolateral half contacts the

posteroventral part of the supraoccipital. The anterodorsal part has two pronounced, acute rims; one medially, the other ventrally. The medial rim forms the dorsolateral lip of the foramen magnum. The ventral rim forms a ridge demarcating the posterodorsal lip of the jugular foramen.

The posteroventral bosses of the exoccipitals form, together with the posterior part of the basioccipital, the occipital condyle. The exoccipitals form the dorsolateral parts of the occipital condyle and the basioccipital the ventral third. The occipital condyle in BP/1/4636 has a central indentation on its articular surface, not described before in *Moschorhinus* (Figs 12, 15). This indentation involves the posterodorsal part of the basioccipital third of the condyle and the posteromedial parts of the exoccipitals. The indentation and the associated lateral bosses hint at a double condyle condition, and are similar to those described by Watson (1913). The suture dividing the exoccipital and the basioccipital runs parasagittally from dorsomedially inside the foramen magnum (see Fig. 12), over the dorsal rim of the occipital condyle, and diagonally to a point ventrolaterally on the convex ventral rim of the occipital condyle. From here the suture runs anteriorly for a short distance on the ventral surface of the occipital condyle and then curves dorsolaterally, over the ventromedial lip of the jugular foramen, from whence it plunges into the jugular foramen in an anterodorsal direction. The dorsomedial side of the posteroventral boss of the exoccipital forms the posterior part of the ventrolateral wall of the foramen magnum (and the concave dorsomedial border of the occipital condyle), and its posterodorsal rim demarcates the posterior border of the foramen magnum. The ventrolateral side of the posteroventral boss forms the ventrolateral border of the occipital condyle, and the anterior border of the ventrolateral side forms the posterior lip of the jugular foramen (Fig. 13). Near the mouth of the jugular foramen, the lateral wall of the posteroventral boss is penetrated by two small foramina for the hypoglossal nerve (XII) (see Fig. 17).

BASIOCCIPITAL (Figs 12, 13, 15–17)

The basioccipital forms the posterior part of the basicranium and the ventral part of the occiput. In ventral view, the basioccipital contacts the basisphenoid anteriorly, the opisthotic laterally, and the exoccipitals posterolaterally.

The anteroventral part of the basioccipital and the posteroventral part of the basisphenoid form the two spheno-occipital tubercles. The suture between the anterior border of the basioccipital and posterior border of the basisphenoid can be seen in ventral view. It dips diagonally in an anteroventral direction from the ventral lip of the fenestra ovalis, curves medially, and surrounds the posterior part of the spheno-occipital tubercle. The suture in the indentation between the two tubercles is set further posteriorly than those parts that bisect the tubercles.

Of the four elements that form the lip surrounding the fenestra ovalis, viz: the basioccipital, opisthotic, basisphenoid and prootic, the basioccipital

contributes least to the formation thereof after the basisphenoid (see Fig. 17). Posterolateral to each speno-occipital tubercle occurs the small laterally directed process of the basioccipitals that forms part of the ventral lip of the fenestra ovalis. This small process is wedged between the posterolateral corner of the basisphenoid anteriorly and the anterior border of the internal process of the opisthotic posteriorly.

The suture between the internal process of the opisthotic and the basioccipital has a roughly diagonal arrangement. Seen in ventral view, it emerges from the fenestra ovalis and runs medially across its ventral surface for a short distance. The suture turns posteromedially and skirts the anterolateral extension of the internal process of the opisthotic, then curves slightly posterolaterally around the ventromedial tuberosity and the posteromedial extension of the internal process of the opisthotic.

Between the posterior border of the internal process of the opisthotic and the posteroventral edge of the occipital condyle, a short parasagittal flange separates the ventrolateral border of the basioccipital and the ventromedial border of the occipital boss of the exoccipital. This suture can be seen in ventral view.

The posterior part of the basioccipital has a rugose ventral surface. This rectangular part of the basioccipital, situated posteriorly to the level of the jugal foramina, forms the convex base of the occipital condyle.

In dorsal view, the posterior part of the basioccipital that participates in the formation of the occipital condyle is visible as a thin strip flanked by the posteroventral bosses of the exoccipitals. The basioccipital is wedge-shaped in occipital view; the broad concave base of the wedge is formed by the ventral surface of the basioccipital. The suture between the basioccipital and exoccipital has been described above.

DISCUSSION

In his paper on the Scaloposauridae, Crompton (1955) described a fused periotic and mentioned that Olson (1944) had not found any dividing suture in the periotic of those therocephalians he had studied either. The specimen known as 'Therocephalian A' (Olson 1944) was discovered in the *Tapinocephalus* zone. Its locality (Boonstra 1969; Kitching 1977) and size indicate that it is most probably a pristerognathid. Olson (1938b) described this specimen as having a periotic, but Boonstra (1954) and Van den Heever (pers. comm.) found a prootic and opisthotic in the Pristerognathidae. It has been shown by Van den Heever & Hopson (1982) that 'Therocephalian B' (Olson 1944) is actually a gorgonopsian. Olson (1944) described a periotic in this specimen, as well as in the other gorgonopsians he studied. Authors such as Sigogneau (1970, 1974) described a prootic and opisthotic in the Gorgonopsia. However, it is possible that, in certain adult Gorgonopsia and Pristerognathidae, the suture between the prootic and opisthotic is difficult or impossible to detect in the region sur-

rounding the fenestra ovalis, but the co-ossification of these elements is not complete enough to consider these groups as having a periotic. The Scaloposauridae also have an opisthotic and prootic as described by Mendrez (1972), and not a periotic as Crompton (1955) described. Neither the Whaitsiidae (pers. obs.) nor the Moschorhinidae have a periotic, a clearly distinguishable prootic and opisthotic being present. It seems quite clear that the Therocephalia have a prootic and opisthotic, and not a periotic.

The pterygoid process of the quadrate, as it is described by Mendrez (1974a), is actually not part of the quadrate but is the posterior end of the quadrate ramus of the pterygoid. The quadrates have been lost in the *Moschorhinus kitchingi* specimen described by Mendrez (1974a) and the specimens described here.

Judging from the shape of the squamosal recess, the quadrate was a relatively large, broad bone, approximately the same shape and size as that described by Mendrez (1974b) in *Promoschorhynchus platyrhinus*. In contrast to the condition understood in *Promoschorhynchus*, the quadrate in *Moschorhinus* seems to have had a small dorsal process that fitted into the quadrate notch of the squamosal (described below). This notch and slot arrangement allowed the quadrate to articulate with the squamosal in a hinge-like manner. The quadrate lay upon the quadrate process of the squamosal and the lateral tip of the quadrate process of the opisthotic that is not covered by the squamosal or pterygoid.

The shape of the quadrate notch of the squamosal indicates that the quadrate had a posterolaterally directed process that articulated medially with the lateral end of the quadrate process of the opisthotic and the quadrate process of the squamosal, and posteriorly with the posterior wall of the quadrate notch that is formed by the squamosal. This process is probably synonymous with the 'squamosal process of the quadrate' described by Mendrez (1974b) in *Promoschorhynchus platyrhinus*. The posteroventral part of the quadrate probably contacted the squamosal in the same manner as in *Promoschorhynchus*. If this was the case, the stapes would be longer than Mendrez (1974a) indicated in *Moschorhinus kitchingi*, and would extend laterally past the lateral end of the opisthotic. The lateral side of the quadrate would have contacted the medial part of the quadratojugal. Because of the absence of the stapes and quadratojugal, it is not possible to describe the relations between these elements and the quadrate.

In her paper on *Moschorhinus*, Mendrez (1974a) referred to the opening dorsal to the posterior apophysis of the epipterygoid and the anterodorsal process of the prootic as the 'foramen veineux'. It would seem that the dorsal part of the anterodorsal process of the prootic is damaged in her specimen. The posterior foramen of the epipterygoid and dorsal venous foramen are separated by the anterodorsal process of the prootic. This process is expanded dorsally to contact the supraoccipital and the posterodorsal process of the epipterygoid. (The term 'dorsal venous foramen' is preferred to venous notch—Boonstra 1934; Cox 1959; dorsal notch—Mendrez 1972; and venous foramen—Mendrez

1974*b*, because it is a foramen completely surrounded by bone, and distinguishes between the two above-mentioned venous foramina.)

The root of the trigeminal nerve (V) exits through the incisura prootica into the cavum epiptericum, which housed the trigeminal ganglion. From this ganglion the three trigeminal rami branched. The ramus ophthalmicus passed mesial to the processus ascendens of the epipterygoid into the orbit. The ramus maxillaris and ramus mandibularis passed posterior to the processus ascendens into the temporal cavity (see Presley & Steel 1976). Certain authors (Brink 1957; Mendrez 1972, 1974*a*, 1974*b*) argue that the posterior apophysis of the epipterygoid divided these two rami. Others (Watson 1920; Kemp 1972) argued that both rami emerged through the foramen dorsal to the posterior apophysis (the posterior foramen of the epipterygoid). Crompton (1955) proposed a third alternative, namely that both rami emerged ventral to the posterior apophysis. The greatest part of the cavum epiptericum (and therefore also the trigeminal ganglion) lies below the level of the posterior foramen of the epipterygoid. Since the ramus maxillaris must have been directed ventrally, as is the ramus mandibularis, it is unlikely that it would first be deflected dorsally from the ganglion to pass through the posterior foramen of the epipterygoid and then ventrally towards the maxilla. It is more feasible that the ramus maxillaris passed, together with the ramus mandibularis, ventral to the posterior apophysis.

The root of the abducens nerve (VI) usually exits through a foramen in the base of the anteroventral process of the prootic (ossified pila antotica) (see Haughton 1918; Goodrich 1958; Starck 1979). In *Moschorhinus* (Mendrez 1974*a*; pers. obs.) and *Promoschorhynchus* (Mendrez 1974*b*) this foramen is absent. Olson (1938*a*) mentioned that a foramen for the abducens nerve may be absent in certain gorgonopsids and would, in this case, pass anterior to the prootic. This seems to have been the case in *Moschorhinus* as well.

The root of the facial nerve (VII) exits through its foramen between the central and ventral ridges of the prootic. No impression for the geniculate ganglion (gasserian ganglion—Mendrez 1972) could be found on the lateral surface of the prootic.

There is no separate glossopharyngeal foramen in *Moschorhinus*. The glossopharyngeal (IX) exited through the jugular canal together with the vago-accessory (X and XI). This is a common feature in the therapsids (see Watson 1911; Haughton 1918; Kemp 1979). The hypoglossal (XII) enters into the jugular foramen through two foramina in its dorsomedial wall (see Fig. 17).

The primary head vein of *Moschorhinus* probably ran mesially to the epipterygoid (see Goodrich 1958; Presley & Steel 1976), then laterally to the otic capsule where it received the vena cerebralis media. This united vessel passed ventral to the paroccipital process of the opisthotic (see Presley & Steel 1976). It is postulated that the vena cerebralis media most probably exited through the incisura prootica via the posterior foramen of the epipterygoid. The posterior foramen of the epipterygoid coincides with the dorsal part of the incisura

prootica, as the anteroventral border of the anterodorsal process of the prootic forms the foramen's posterior border (see Fig. 16). If the vena cerebialis media passed through this foramen, it would be in line with the dorsal opening of the pterygo-paroccipital foramen through which it would pass ventrally to join the primary head vein. Many authors (Watson 1920; Parrington 1946; Cox 1959; Fourie 1974) described a groove running from the pterygo-paroccipital foramen to the incisura prootica (foramen for the trigeminal nerve—Parrington 1946). Most authors since Watson (1920) have claimed that the vena capitis lateralis ran in this groove, but it seems unlikely that this large vein could pass through the small posterior foramen of the epipterygoid in *Moschorhinus*. Moreover, the vena cerebialis media, which is a very important vein in extant reptiles (usually ignored by these writers), must have left some trace on the lateral wall of the prootic.

The vena capitis dorsalis, which was situated in the sinus canal in cynodonts (Watson 1911), seems to have been expanded anteriorly to form a broad sinus that was situated in the lateral supraoccipital fossa in *Moschorhinus*. This sinus would have been confluent anteriorly with a vein that passed through the dorsal venous foramen. The vena capitis dorsalis would have been connected to the vein that passed through the pterygo-paroccipital foramen (probably the vena cerebialis media) and the vein that passed through the post-temporal fenestra (see Watson 1920; Parrington 1946; Cox 1959; Fourie 1974).

The internal carotid artery ran anteriorly, ventral to the paroccipital process of the opisthotic, and entered the external opening of the parabasal canal. The stapelial artery branched off from the internal carotid in the proximity of the stapes. It probably ran in an anterodorsal direction in the depression below the central ridge of the prootic towards the cavum epipterygium, where it ramified into three branches, each of which accompanied a trigeminal nerve ramus (see O'Donoghue 1920).

Moschorhinus has many primitive characteristics, such as large suborbital vacuities similar to those of the pristerognathids (see Boonstra 1969), a gorgonopsid-like dentition (see Parrington 1955), and a robust skull compared to other Therocephalia (see Crompton 1955; Romer 1956; Brink 1959). Its epipterygoid is not as expanded, and therefore not involved to the same degree in the formation of the lateral wall of the braincase as are those of *Promoschorhynchus* (Mendrez 1974b) or whaitsiids (Kemp 1972). No ossified ethmoid or orbitosphenoid elements could be found, as in gorgonopsids (see Olson 1944; Kemp 1969) or in whaitsiids (see Kemp 1972). *Moschorhinus* has large post-temporal fenestrae compared to cynodonts (see Watson 1920; Romer 1969; Kemp 1979), but this may be a characteristic peculiar to the Therocephalia (see Kemp 1972) because they are also larger than those of primitive therapsids (see Romer 1956).

Derived and advanced characteristics in *Moschorhinus* include the paroccipital fossa of the opisthotic, which seems to be shared with all the other therocephalians except the pristerognathids (see Hopson & Barghusen 1986).

The epipterygoid and its relations with the surrounding bony elements are more advanced in *Moschorhinus* than in primitive Therocephalia (see Boonstra 1934; Crompton 1955; Mendrez 1972). *Moschorhinus* has a much larger epipterygoid than the gorgonopsids, scaloposaurids or certain pristerognathids. Its epipterygoid makes sutural contact with the parietal and supraoccipital dorsally and the prootic posterodorsally, thus forming a substantial part of the lateral wall of the braincase. The posterior apophysis of the epipterygoid is present in certain Therocephalia (see Brink 1957; Kemp 1972; Mendrez 1974b), but in *Moschorhinus* it most probably made contact with the prootic, a condition unique amongst the Therocephalia. The posterior foramen of the epipterygoid is shared with the whaitsiids (see Kemp 1972). The venous notch of the primitive therapsids (see Boonstra 1934; Olson 1937; Mendrez 1972) is closed anteriorly by the epipterygoid in *Moschorhinus* forming a venous foramen, as happens in whaitsiids (see Kemp 1972).

Looking at all the above-mentioned characteristics it would seem that *Moschorhinus* was more advanced than the pristerognathids or scaloposaurids. *Moschorhinus* was more primitive than, but not ancestral to, the whaitsiids. *Moschorhinus* has a more primitive palatine region (see Mendrez 1974a), large suborbital vacuities, postcanines, and a robust skull. *Theriognathus*, on the other hand, does not possess suborbital vacuities nor postcanines and has a more delicate skull. *Moschorhinus* did not have an ossified orbitosphenoid or interorbital septum as in whaitsiids. Its epipterygoid is also much smaller and participates less in the formation of the lateral wall of the braincase (see Kemp 1972). The posterior foramen of the epipterygoid may have a different function in *Moschorhinus* than in whaitsiids, because in *Moschorhinus* it is formed differently and the posterior apophysis in the whaitsiid described by Kemp (1972) obstructs the passage between the posterior epipterygoid foramen and the pterygo-paroccipital foramen. In whaitsiids the posteroventral process of the epipterygoid (quadrate ramus of the pterygoid—Kemp 1972) is also apparently much closer to the prootic than in *Moschorhinus*.

Moschorhinus has too many derived characteristics to be a cynodont ancestor. It has paroccipital fossae, large post-temporal fenestrae and suborbital vacuities. It has few postcanine teeth, a small dorsal parietal foramen and, as in all Therocephalia, no stapedia foramen (see Mendrez 1974a). Furthermore, the posterior epipterygoid foramen is unique to the moschorhinids and the whaitsiids, and not homologous to the cynodont trigeminal foramen.

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REFERENCES

- BOONSTRA, L. D. 1934. A contribution to the morphology of the mammal-like reptiles of the suborder Therocephalia. *Annals of the South African Museum* **31** (2): 215–267.
- BOONSTRA, L. D. 1954. The pristerognathid therocephalians from the *Tapinocephalus*-zone in the South African Museum. *Annals of the South African Museum* **42** (2): 65–107.
- BOONSTRA, L. D. 1969. The fauna of the *Tapinocephalus* zone (Beaufort beds of the Karoo). *Annals of the South African Museum* **56** (1): 1–73.
- BRINK, A. S. 1951. Studies of Karroo reptiles. 1. Some small cynodonts. *South African Journal of Science* **47** (12): 338–342.
- BRINK, A. S. 1957. On *Aneugomphius ictidoceps* Broom and Robinson. *Palaeontologia africana* **4**: 97–115.
- BRINK, A. S. 1959. Notes on some whaitsiids and moschorhinids. *Palaeontologia africana* **6**: 23–49.
- BROOM, R. 1920. On some new therocephalian reptiles from the Karoo Beds of South Africa. *Proceedings of the Zoological Society of London* **2** (18): 343–355.
- BROOM, R. 1935. On some new genera and species of Karoo fossil reptiles. *Annals of the Transvaal Museum* **18** (1): 55–72.
- BROOM, R. 1938. The origin of the cynodonts. *Annals of the Transvaal Museum* **19** (2): 279–288.
- COX, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proceedings of the Zoological Society of London* **132** (3): 321–367.
- CROMPTON, A. W. 1955. A revision of the Scaloposauridae with special reference to kinetism in this family. *Navorsinge van die Nasionale Museum* **1** (7): 149–183.
- DE BEER, G. 1937. *The development of the vertebrate skull*. Oxford: Oxford University Press.
- FOURIE, S. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Annals of the South African Museum* **65** (10) 337–400.
- GOODRICH, E. S. 1958. *Studies on the structure and development of vertebrates*. New York: Dover.
- HAUGHTON, S. H. 1918. Some new carnivorous Therapsida, with notes upon the brain-case in certain species. *Annals of the South African Museum* **12** (6): 175–216.
- HOPSON, J. A. & BARGHUSEN, H. R. 1986. An analysis of therapsid relationships. In: HOTTON, N. ET AL. eds. *The ecology and biology of mammal-like reptiles*. Washington, D.C.: Smithsonian Institution Press.
- HOPSON, J. A. & CROMPTON, A. W. 1969. Origin of mammals. *Evolutionary Biology* **3** (2): 15–72.
- KEMP, T. S. 1969. On the functional morphology of the gorgonopsid skull. *Philosophical Transactions of the Royal Society (B)* **256** (801): 1–8.
- KEMP, T. S. 1972. Whaitsiid Therocephalia and the origin of cynodonts. *Philosophical Transactions of the Royal Society (B)* **264** (857): 1–54.
- KEMP, T. S. 1979. The primitive cynodont *Procynosuchus*: functional anatomy of the skull and relationships. *Philosophical Transactions of the Royal Society (B)* **285** (1005): 73–122.
- KEMP, T. S. 1982. *Mammal-like reptiles and the origin of mammals*. London: Academic Press.
- KERMACK, D. M. & KERMACK, K. A. 1984. *The evolution of mammalian characters*. USA: Kapitaan Szabo.
- KITCHING, J. W. 1977. The distribution of the Karoo vertebrate fauna. *Memoirs. Bernard Price Institute for Palaeontological Research* **1**: 1–131.
- MENDREZ, C. H. 1972. On the skull of *Regisaurus jacobi*, a new genus and species of Bauriarmorpha Watson and Romer, 1956 (= *Scalopsauria* Boonstra, 1953), from the *Lystrosaurus*-zone of South Africa. In: JOYSEY, K. A. & KEMP, T. S. eds. *Studies in vertebrate evolution*: 191–212. Edinburgh: Oliver & Boyd.
- MENDREZ, C. H. 1974a. Étude du crâne d'un jeune specimen de *Moschorhinus kitchingi* Broom, 1920 (? *Tigrisuchus simus* Owen, 1876), Therocephalia, Pristerosauria, Moschorhinidae d' Afrique australe. (Remarques les Moschorhinidae et les Whaitsiidae.) *Annals of the South African Museum* **64**: 71–115.